

THE GENUS *TYCHIUS* GERMAR (COLEOPTERA:  
CURCULIONIDAE): LARVAE AND PUPAE OF SOME  
SPECIES, WITH EVALUATION OF THEIR  
CHARACTERS IN PHYLOGENETIC ANALYSIS<sup>1</sup>

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*Abstract.*—Larvae of eight species and pupae of five species of North American *Tychius* are described. Of these, only the larvae of *T. picirostris* (Fabricius) and *T. stephensi* Schönherr, have been previously described. Larvae of the European *T. quinquepunctatus* (L.) and *T. flavicollis* Stephens, also described, are compared to larvae of the North American species and to other European species known from previously published descriptions. Larval and pupal characters appear to support some groupings previously postulated on the basis of morphological characters of adults and host plant relationships. However, because of the lack of structural complexity in known characters of *Tychius* immatures, and the apparent lack of major differences between many of the species in these stages, it appears that the larval and pupal characters do not provide strong evidence of phylogenetic relationships. Superficial similarity due to parallelism or convergence appears likely in some cases. The hypothesis of polyphyly of the genus *Miccotrogus* Schönherr is not refuted by characters of the immature stages of some of the species formerly assigned to that taxon.

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Since revision of the North American species of *Tychius* (Clark, 1971), the senior author has continued studies of members of that genus and of the related genus *Sibinia*. A classification of the subfamily Tychiinae (Clark et al., 1977), including the genera *Tychius* and *Sibinia*, provides a framework for research on the group. Relationships of North American *Tychius* to members of the much larger Old World, primarily Palearctic, *Tychius* fauna are discussed by Clark (1976, 1977). A revised classification of native North American *Tychius* and host and distributional records for these are also included in the 1977 paper. Clark and Burke (1977) present notes on life histories and habits of native North American *Tychius* and review biology of world members of the genus which consists of more than 300 nominate species, several of which are of economic importance (see Muka, 1954; Hoffmann et al., 1963; Yunus and Johansen, 1967; Nasredinov, 1975). Similar information on members of the genus *Sibinia* is presented by Clark (1978a).

Most published descriptions and illustrations of immature stages of members of the genus *Tychius* are not sufficiently detailed to be taxo-

nomically useful. Exceptions are those of *T. quinquepunctatus* (L.) by Grandi (1916) and Scherf (1960), and *T. flavus* Becker by Servadei (1947). Scherf (1964) also assembled information from numerous sources on bionomics and immature stages of Curculionoidea, including several species of *Tychius*, of Central Europe. These and other publications (see Burke and Anderson, 1976) have been searched for taxonomic characters of *Tychius* larvae and pupae, and these characters are compared with the ones revealed by our own observations. In this paper we describe larvae of 6 of the 12 known native North American species of *Tychius* and pupae of 4 of these, larvae of 2 European species introduced into North America and the pupa of one of these, and larvae of 2 other European members of the genus. The usefulness of the larval and pupal characters described in recognizing monophyletic groups within the genus has also been analyzed.

#### Materials and Methods

As Ahmad and Burke (1972) and Burke and Anderson (1976) pointed out, systematic studies of immature Curculionidae, as well as of other Coleoptera, have not progressed as rapidly as studies based on adults. This is due in part to the relative difficulty encountered in obtaining specimens of the immature forms and the more time-consuming procedures necessary to prepare larvae for study. Timing is the critical factor in obtaining *Tychius* larvae and pupae. Larvae suitable for taxonomic study are available for only a short period when fruits of their hosts, members of the legume subfamily Papilionoideae, are mature. Once infested fruits are found, however, larvae may be obtained relatively easily by placing the pods in porcelain pans. When larvae emerge from infested pods they may be transferred to a mixture of sand and peat moss in widemouth glass jars. The larvae tunnel into the substrate, pupate and complete their development to the adult stage there (see Clark and Burke, 1977).

Larvae of 8 and pupae of 5 of the 14 species of *Tychius* known to occur in North America have been collected. Larvae and pupae were preserved in 70% ethyl alcohol; a few reared adults were also preserved with the immatures to facilitate subsequent identification. When larvae were collected but pupae and adults were not subsequently reared, identification was based upon association with adults taken on plants from which the larvae were obtained.

Larvae of some species were obtained for study through loans from the Ohio State University (OSU), the U.S. National Museum (USNM), and from Dr. C. A. Johansen, Washington State University (collections are referred to in the text by the abbreviations in parentheses); specimens collected by Clark are deposited in the collections of the Department of

Entomology, Texas A&M University (TAM) and in the USNM. For some of the borrowed material, larvae and pupae were identified by association with accompanying adults, even when there was no direct evidence that the adults were reared from larvae from the same lot. When no adults were present, reliance was placed upon determination labels with the immatures, even though there was usually no indication as to how these determinations were made.

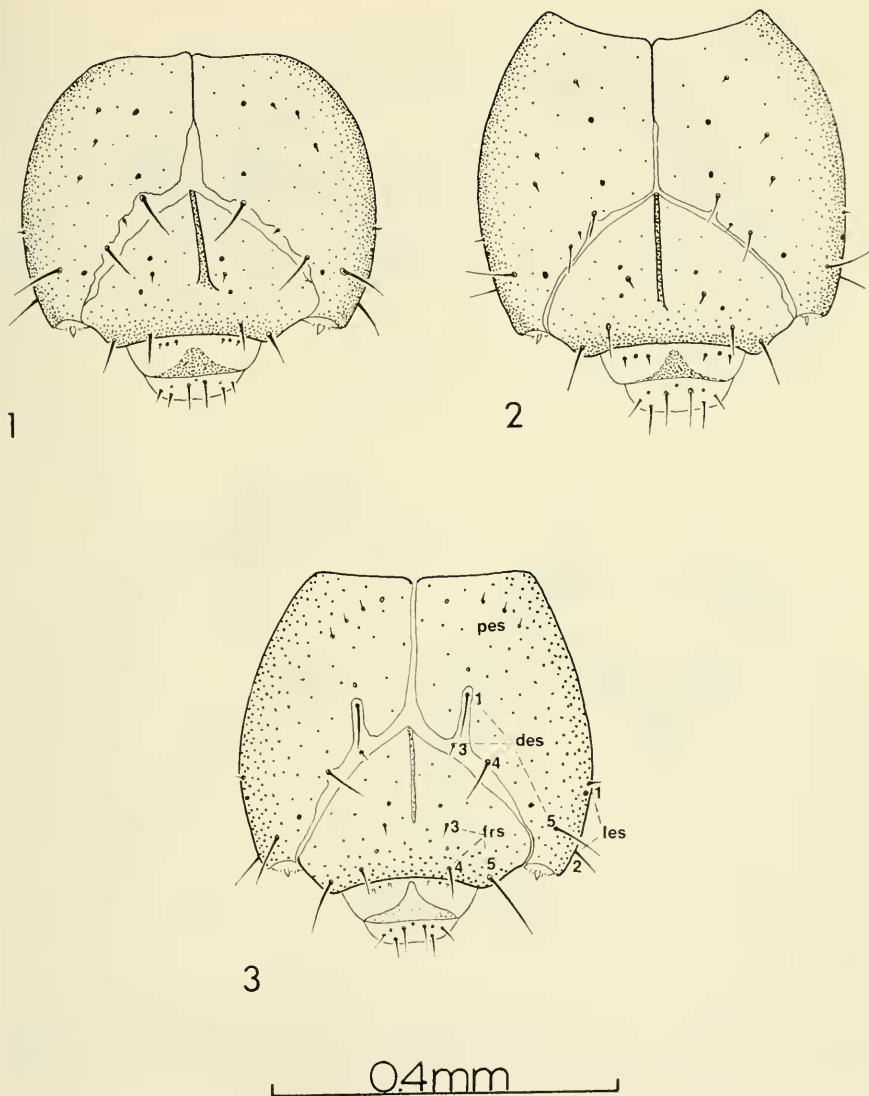
Pupae and entire larvae were examined in alcohol, but examination of most larval characters required that the specimens be slide-mounted. Except for a few modifications, slides were prepared by the procedures described by Ahmad and Burke (1972). It was found to be easier to remove the mouthparts from the head capsule before removing the latter from the body. Mounting and examination were also easier when the 2 sides of the larval skin remained broadly intact mid-dorsally than when the two halves were completely separated. Hoyer's was used as the mounting medium. Drawings were made by procedures outlined by Ahmad and Burke (1972).

Anderson (1947) is followed for terminology of larval characters. Where applicable, pupal terminology proposed by Burke (1968) is used. In the text the setae on only 1 side of the body are described.

## Descriptions

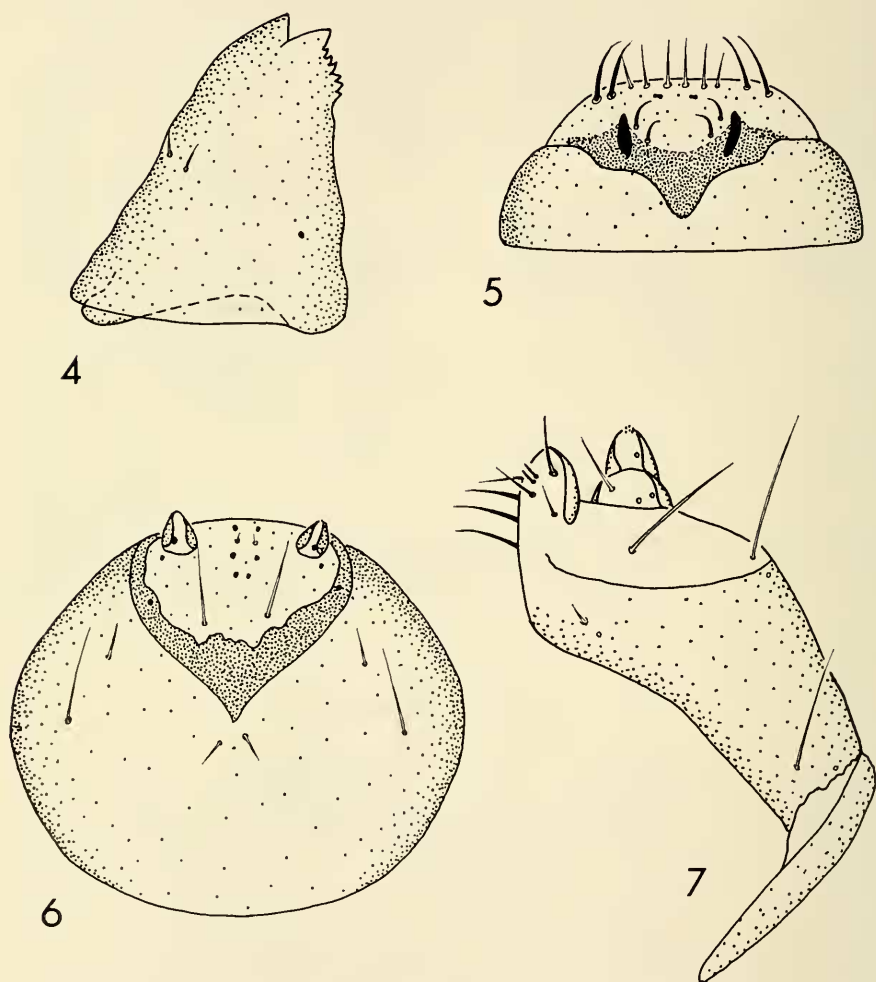
### Genus *Tychius* Germar

*Larva*.—Body (Fig. 8): Elongate, slightly curved; integument rugulose in large species, smooth in smaller ones; larger species with transverse rows of fine asperities on ventral portions of thoracic and 1st few abdominal segments. Head (Figs. 1–7): Free, wider than long, narrowed slightly anteriorly; anterior ocelli present. Antenna with membranous basal article bearing a blunt to elongate, acute accessory appendage and several minute sensory processes. Hypopharyngeal bracon distinct. Frontal sutures distinct throughout length, incomplete anteriorly. Epicranial suture less than  $\frac{1}{2}$  as long as head capsule. Frons bearing 3 pairs of setae, setae 1 and 2 absent, seta 3 short to minute, seta 4 long, but shorter than seta 5; 2 pairs of frontal sensilla, 1 pair between frontal setae 3 and 4, the other anterior, lateral, or posterior to seta 3. Dorsal epicranial seta 1 minute or long, setae 4 and 5 long, seta 3 short, located on or slightly posterior to frontal suture between setae 1 and 4, seta 2 absent; 1 sensillum located between dorsal epicranial setae 4 and 5 on each side, another just posterior to seta 1. Lateral epicranium with 2 pairs of setae, seta 1 short, seta 2 longer; 1 pair of sensilla located anterior to seta 1. Ventral epicranium with 2 pairs of short setae. Posterior epicranium with 2 or 3 pairs of minute setae and 2 pairs of



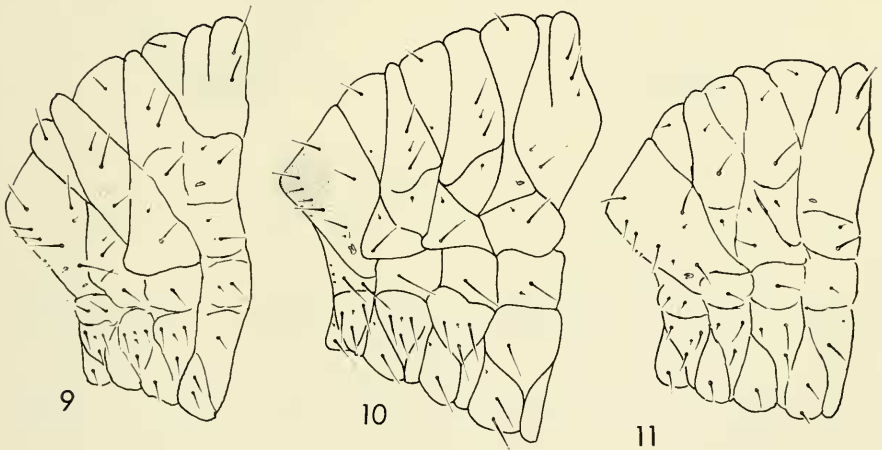
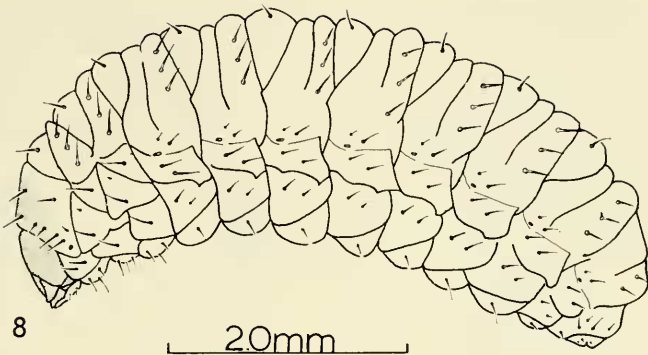
Figs. 1-3. Dorsal views of head capsules of larval *Tychius*. 1, *T. sordidus*. 2, *T. lineellus*. 3, *T. quinquepunctatus*.

sensilla. Clypeus wider than long, with 2 pairs of minute setae and 2 sensilla, each 1 of which is located between or slightly distad of clypeal setae on each side. Labrum (Figs. 1-3) with 3 pairs of setae, seta 3 shorter than seta 2; labral sensilla present, median labral sensillum present or absent. Epipharynx (Fig. 5) with 2 anterolateral setae on each side, 6



Figs. 4-7. Mouth parts of *Tychius sordidus*. 4, Left mandible, dorsal view. 5, Epipharynx; 6, Labium, ventral view. 7, Right maxilla, ventral view.

anteromedian setae, and 4 medium spines; 2 pairs of epipharyngeal sensilla present. Labral rods short, stout, widely separated. Mandible (Fig. 4) with 2 apical teeth, 2 mandibular setae and 1 sensillum. Maxillary palpus (Fig. 7) consists of 2 articles; apical article with 1 sensillum and an apical cluster of minute papillae; basal article shorter than apical article, bearing 1 seta, 2 sensilla. Labium (Fig. 6), palpus consists of 1 article; premental sclerite with anterior and posterior median extensions obsolete; prementum



Figs. 8–11. Lateral views of larval *Tychius*. 8, *T. sordidus*. 9, *T. stephensi* (thoracic and 1st abdominal segments). 10, *T. tectus* (thoracic and 1st abdominal segments). 11, *T. tectus* (thoracic and 1st abdominal segments).

with 1 pair of long setae and 1 pair of sensilla; glossa with 1 or 2 pairs of short to minute setae and 2 or 3 pairs of medial sensilla, and 1 sensillum located near base of each labial palpus; postmentum with 2 or 3 pairs of setae, seta 1 short or absent, seta 2 long, seta 3 shorter than 2. Thorax (Figs. 8–11): Not narrower than abdomen. Pronotum with 7–8 minute to long setae and 2 minute setae on anterolateral margins. Thoracic spiracle unicameral or bicameral. Prodorsum and epipleural lobe of mesothorax and metathorax each with 1 long seta. Pleural area of prothorax with 2

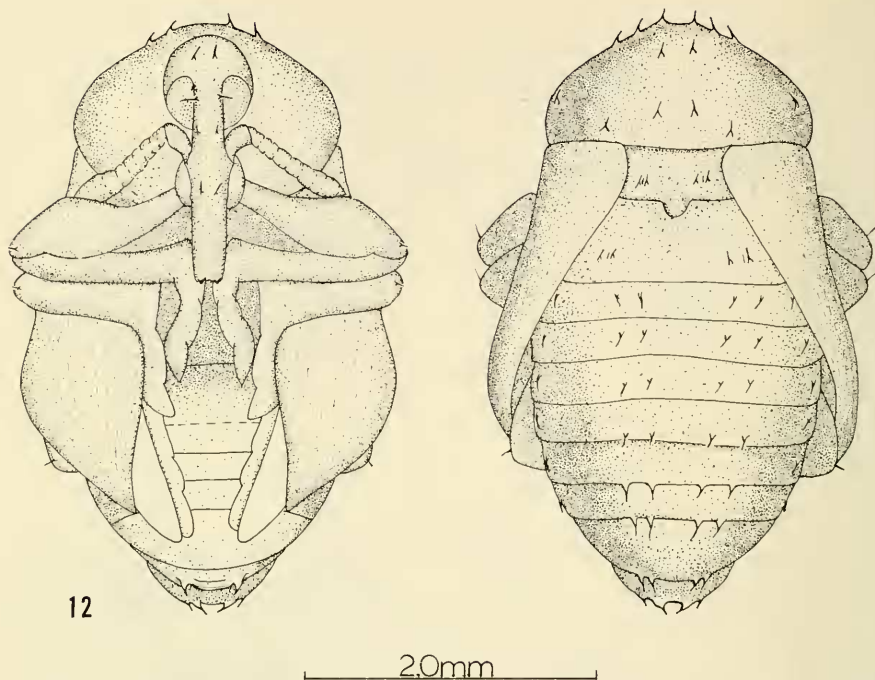


Fig. 12. Pupa of *Tychius sordidus*, ventral view on left, dorsal view on right.

long setae, and with 3 minute setae on extreme anteromedian margin; pleural area of mesothorax and metathorax each with 1 long seta. Sternum of each thoracic segment with 1 moderately long seta and 1 minute seta. Abdomen (Figs. 8-11): 8 pairs of lateral, unicameral spiracles. Segments I-VII each with 3 dorsal folds, prodorsal fold more prominent than postdorsal; segment VIII with 2 dorsal folds. Segments I-VII each with 1 long prodorsal seta and 2-3 postdorsal setae. Epipleurum with 1 long and 1 shorter seta. Pleural area with 1 long and 1 shorter seta. Pedal areas each with 1 long seta. Eusternum with 2 long setae. Segment IX with 1 postdorsal seta, 1 short and 1 longer epipleural setae, 1 short and 1 longer pleural setae and 1 short and 1 longer eusternal setae. Sternellum distinct. Anus terminal, anal folds bearing a few minute setae.

*Pupa* (Fig. 12).—Head: Distirostral setae absent. Two pairs of basirostral setae, 1 pair located just distad of ocular area, the other directly over the point of antennal insertions, proximal pair usually longer than distal pair, each borne on summit of rounded to conical tubercle. One pair of interorbital setae, each seta borne on summit of conical tubercle; interorbitals longer and stouter than basirostrals. Supraorbital setae absent. One or

2 pairs of frontal setae present, each seta borne on summit of conical tubercle; frontals about same length as interorbitals. Pronotum: 1 pair of anteromedian setae; 2 pairs of anterolateral setae; 1 pair of discal setae located directly posterior to anteromedian setae, sometimes more widely separated than anteromedians; 1 pair of posteromedian setae, and 1 or 2 pairs of posterolateral setae. Mesonotum and Metanotum: Anteronotal setae absent. One to 3 pairs of posteronotal setae; when 2 or more pairs present, setae on each side close together, borne on separate tubercles or on common tubercle; 3rd seta when present not borne on tubercle. Abdomen: Anterotergal setae absent. One to 3 pairs of discotergal setae, each seta borne on summit of conical tubercle, tubercles becoming larger posteriorly. One pair of laterotergal setae on terga 1-7 or 8, each seta borne on summit of low, indistinct tubercle. Segment 9 with a pair of short, sharply pointed, widely separated posterior processes. Abdomen devoid of ventral setae. Femora: Bearing 1 or 2 setae, or without setae; when only 1 seta present it is borne on outer face near apex, 2nd seta if present borne on dorsal surface near apex.

*Material examined.*—The larval description is based upon examination of larvae of *T. sordidus* LeConte, *T. lineellus* LeConte, *T. tectus* LeConte, *T. semisquamosus* LeConte, *T. soltaui* Casey, *T. prolixus* Casey, *T. quinquepunctatus*, *T. stephensi* Schönherr, *T. picirostris* (Fabricius) and *T. flavicollis* Stephens, and published descriptions of *T. flavus* (Servadei, 1947; Scherf, 1964), *T. meliloti* Stephens, and *T. crassirostris* Kirsch (Scherf, 1964). The pupal description is based on examination of pupae of *T. sordidus*, *T. tectus*, *T. soltaui*, *T. prolixus* and *T. picirostris* and on published descriptions of *T. quinquepunctatus* (Scherf, 1964), *T. flavus* (Servadei, 1947; Scherf, 1964) and *T. meliloti* and *T. crassirostris* (Scherf, 1964).

*Discussion.*—Known *Tychius* larvae are distinguished from larvae of *Sibinia sulcatula* (Casey) (Rogers et al., 1975), and *S. sodalis* Germar (Scherf, 1964), by the following combination of characters: Dorsal epicranial seta 1 long (except *T. picirostris*); dorsal epicranial seta 3 short, located on or slightly posterior to frontal suture between dorsal epicranial setae 1 and 4; epipharynx with 2 instead of 3 sensory pores; mandible with 2 rather than 3 apical teeth; abdominal prodorsal seta long; spiracular seta 2 long. Known pupae of *Tychius* members can be distinguished from the pupa of *S. sulcatula* by the number of posterolateral pronotal setae; 1 or 2 in *Tychius*, 4 in *S. sulcatula*. Scherf's (1964) description of the pupa of *S. sodalis* does not clearly indicate the number of posterolateral setae.

The larvae and pupae of the species listed above under the material examined heading are each described below; characters cited in the generic description are omitted. The diagnostic characters of the larvae are listed in Table 1, those of the pupae in Table 2.



Table 1. Summary of selected larval characters showing distribution among some species of *Tychius*.

Larval Character States		<i>sordidus</i>	<i>lineellus</i>	<i>tectus</i>	<i>semisquamosus</i>	<i>soltani</i>	<i>prolixus</i>	<i>quinquepunctatus</i>	<i>flavicollis</i>	<i>stephensi</i>	<i>picrostris</i>	<i>flavus</i>	<i>meliloti</i>
Dorsal epicranial seta 1	short										X		
	long	X	X	X	X	X	X	X	X	X		X	
Median labral sensillum	present	X	X	X	X	X	X	X	X	X		X	
	absent										X		
Dorsal malar setae	3									X	X		
	4	X	X	X	X	X	X	X	X				
Sensilla labial palpus	1	X		X	X	X	X	X	X				
	2		X							X	X		
Pairs glossal setae	1	X	X	X	X	X		X					
	2							X		X	X		
Long pronotal setae	5	X	X	X	X	X	X	X	X				
	4									X	X	X	
Thoracic spiracle	unicameral									X		X	X
	bicameral	X	X	X	X	X	X	X	X		X		
Thoracic postdorsal setae	2									X	X	X	
	3	X	X	X	X	X	X	X	X				
Alar setae	short		X	X	X	X	X	X	X	X	X		
	long	X											
Epipleural seta 2	short		X	X	X	X	X	X	X	X	X		
	long	X											
Pleural setae	1										X		
	2	X	X	X	X	X	X	X	X	X			

*Tychius sordidus* LeConte

Figs. 1, 4-8, 12

*Tychius sordidus* LeConte, 1876:217.

*Larva*.—Body: 4.6-6.6 mm long (40 larvae); shining, yellow. Head (Fig. 1): Uniformly dark yellowish brown; truncate posteriorly; width of

Table 2. Summary of selected pupal characters showing distribution among some species of *Tychius*.

Pupal Character States		<i>sordidus</i>	<i>tectus</i>	<i>soltani</i>	<i>prolixus</i>	<i>quinque-punctatus</i>	<i>flavicollis</i>	<i>stephensi</i>	<i>picrostris</i>	<i>flavus</i>	<i>meliloti</i>	<i>crassirostris</i>
Anterolateral setae of pronotum (pairs)	2 3	X X	X X	X X	X X	X X			X X		?	?
Posterolateral setae of pronotum (pairs)	1 2	X X	X X	X X	X X	X X			X X		?	
Posteronotal setae of pronotum (pairs)	1 1-2	X X	X X	X X	X X	X X			X X			
Discotergal setae of abdomen (pairs)	1 2		X X	X X	X X	X X			X X		?	X
Femoral setae	1 2	X X		X X		X X			O X	X X		X

head capsule 0.82–0.94 mm (8 larvae). Ocellar areas lacking subcutaneous pigment. Accessory appendage of antenna robust, sides rounded. Endocarina more than  $\frac{1}{2}$  as long as frons. Dorsal epicranial seta 1 long. Median labral sensillum present. Malar area of maxilla (Fig. 7) with 5 ventral and 4 dorsal setae. Labial palpus (Fig. 6) with 1 sensillum; glossa with 1 pair of minute setae; postmental seta 1 present. Thorax (Fig. 8): Pronotum with 5 long setae, 2 moderately long setae, 1 short seta and 2 minute anterolateral setae. Spiracle bicameral, air tubes each with 5 to 8 annuli. Postdorsum of mesothorax and of metathorax each with 3 long setae. Pedal area of each thoracic segment with 3 long and 3 minute to moderately long setae. Sternal seta slightly shorter than ventralmost pedal seta of the same segment. Abdomen (Fig. 8): Postdorsum with 3 long setae of subequal length. Spiracular seta 1 long, seta 2 shorter. Epipleural seta 1 slightly shorter than seta 2. Pleural seta 2 slightly shorter than seta 1.

*Pupa* (Fig. 12).—Length: 3.9–5.0 mm (25 pupae). Head: Distalmost pair of basirostral setae absent in some specimens. Pronotum: 2 pairs of posterolateral setae. Mesonotum and Metanotum: 1–3 pairs of posteronotal setae. Abdomen: 2 pairs of discotergal setae on terga 1–5; terga 6 and 7 often each with 3 pairs of setae, tergum 8 usually with 1 pair, but sometimes with 2 pairs of discotergals. Legs: Femur with 1 seta or without a seta.

*Material examined*.—Fifty larvae (40 entire, 10 slide-mounted specimens, TAM, USNM), which emerged from pods of *Baptisia leucophaea* Nutt. var. *laevicollis* (Gray) Small, collected 10 May 1973, at College Station, Brazos County, Texas, and 25 pupae (TAM, USNM), laboratory reared from larvae from the same pods, all determined by association with reared adults.

*Discussion*.—*Tychius sordidus* occurs in the eastern and midwestern United States. Its known hosts are all members of the plant genus *Baptisia* (Clark, 1971; Clark and Burke, 1977). The larva is distinguished from that of other members of the genus by the following combination: Alar area of each thoracic segment with 1 long seta; mesothorax and metathorax each with 3 long postdorsal setae of subequal length. The pupa is distinguished as follows: Femoral setae 1 or none; posteronotal setae 1–3 pairs; discotergal setae 2 pairs.

*Tychius lineellus* LeConte

Fig. 2

*Tychius lineellus* LeConte, 1876:217.

*Larva*.—Body: 5.7–6.8 mm long (3 larvae); opaque, pale yellowish white. Head (Fig. 2): Uniformly dark brown; emarginate posteriorly; width of head capsule 0.74–0.84 mm (5 larvae). Ocellar areas with subcutaneous pigment. Accessory appendage of antenna moderately long, sides slightly rounded. Endocarina more than  $\frac{1}{2}$  as long as frons. Dorsal epicranial seta 1 long. Labral setae 1 and 2 subequal in length. Median labral sensillum present. Malar area of maxilla with 5 ventral and 4 dorsal setae and 1 ventral sensillum. Labial palpus with 2 sensilla; glossa with 1 pair of minute setae; postmental seta 1 present. Thorax: Pronotum with 5 long setae, 2 shorter setae and 1 minute seta, in addition to 2 minute anterolateral setae. Spiracle bicameral, air tubes with 5 to 8 annuli. Postdorsum of mesothorax and of metathorax with 3 setae, seta 3 long, seta 2 very short, seta 1 intermediate in length. Pedal area of each thoracic segment with 3 long and 3 minute to moderately long setae and a few sensilla. Sternal seta slightly shorter than ventral-most pedal seta of the same segment. Abdomen: Postdorsum with 3 setae, setae 1 and 3 slightly shorter than seta 2. Spiracular seta 1 long, seta 2 slightly shorter. Epipleural seta 1 slightly shorter than seta 2. Pleural seta 2 slightly shorter than seta 1.

*Pupa*.—Unknown.

*Material examined*.—Eight larvae (3 entire, 5 slide-mounted specimens, TAM, USNM), which emerged from pods of *Lupinus leucophyllus* Dougl., collected 6 July 1968, 5 miles east of Springville, Utah County, Utah, determined by association with adults collected on the plants.

*Discussion*.—*Tychius lineellus* occurs in the western United States and

adjacent portions of Canada. Its known hosts are members of the plant genus *Lupinus* (Clark, 1971). The larva is distinguished from larvae of other species of *Tychius* by the following combination: Labial palpus with 2 sensilla; mesothorax and metathorax each bearing 3 setae, setae 1 and 2 short, seta 3 long. It also has a sensillum on the malar area of the maxillary palpus, as does the Old World *T. quinquepunctatus*. Adult characters do not indicate a close relationship between *T. lineellus* and *T. quinquepunctatus*, however.

*Tychius tectus* LeConte

Fig. 10

*Tychius tectus* LeConte, 1876:217.

*Tychius mixtus* Hatch, 1971:355.

*Larva*.—As described for *T. sordidus*, except as follows. Body: 5.5–5.8 mm long (8 larvae); pale yellowish white to yellow. Head: Uniformly light yellowish brown; posteriorly truncate; width of head capsule 0.60–0.67 mm (4 larvae). Ocellar areas lacking subcutaneous pigment. Accessory appendage of antenna short, sides rounded. Endocarina distinct, more than  $\frac{1}{2}$  length of frons. Dorsal epicranial seta 1 long. Labral seta 1 longer than seta 2. Median labral sensillum present. Malar area of maxilla with 5 ventral and 4 dorsal setae. Labial palpus with 1 sensillum; postmental seta 1 present. Thorax (Fig. 10): pronotum with 5 long setae, 2 moderately long setae, and 1 minute seta, in addition to 2 minute anterolateral setae. Spiracle bicameral, air tubes with 4 to 6 annuli. Postdorsum of mesothorax and of metathorax with 3 setae; setae 1 and 3 long, seta 2 minute. Pedal area of each thoracic segment with 3 long setae, 1 short to minute seta, and 1 sensillum. Sternal seta long, subequal in length to ventral-most seta of pedal area of same segment. Abdomen (Fig. 10): Postdorsum with 3 setae, setae 1 and 2 longer than seta 3. Spiracular seta 1 long, seta 2 very short. Epipleural seta 1 much shorter than seta 2. Pleural seta 2 much shorter than seta 1.

*Pupa*.—The pupa of *T. tectus* differs from that of *T. sordidus* in its smaller size (length 2.9–3.4 mm) and by possession of the lowermost pair of basirostral setae, 2 femoral setae, 1 or 2 pairs of mesonotal and metanotal posteronotal setae and 1 pair of discotergal setae on terga 1–8.

*Material examined*.—Twelve larvae (8 entire, 4 slide-mounted specimens, TAM, USNM), from pods of *Astragalus distortus* var *engelmannii* (Sheldon) Jones, collected 5 May 1972, at College Station, Brazos County, Texas and 3 pupae (TAM, USNM), laboratory-reared from other larvae taken from the same plants at the same time, all determined by association with reared adults.

*Discussion*.—*Tychius tectus* is widely distributed throughout the Great

Plains and Rocky Mountain regions of the western United States and adjacent portions of Canada (Clark, 1971 and 1977). Its hosts, members of the papilionoid tribe Astragaleae, include species of *Astragalus* in primarily Eurasian groups, members of the same genus in autochthonous American groups, and species of *Oxytropis*, a primarily Eurasian genus closely related to *Astragalus* (Clark, 1977). The larva is distinguished from larvae of other members of the genus as follows: Mesothorax and metathorax each with 3 postdorsal setae, setae 1 and 3 long, seta 2 short; typical abdominal segments also with 3 postdorsal setae, setae 1 and 2 long, seta 3 short. Distinguishing characters of the pupa are listed above.

The larvae and pupae of most of the other American Astragaleae-associated *Tychius* are either apparently identical to those of *T. tectus*, or are distinguished only by minor, in some cases variable characters (these are enumerated in the discussions of *T. semisquamosus*, *T. soltaui* and *T. prolixus*, which follow). The close similarity of these species to each other supports the contention that the Astragaleae-associated *Tychius* form a monophyletic (possibly paraphyletic) group (Clark, 1977).

*Tychius semisquamosus* LeConte

*Tychius semisquamosus* LeConte, 1876:217.

*Tychius lamellosus* Casey, 1892:418.

*Tychius squamosus* Hatch, 1971:356.

*Tychius intermixtus* Hatch, 1971: 356.

*Larva*.—The larva of *T. semisquamosus* has subcutaneous pigment on the ocellar areas and fine asperities on the thoracic and abdominal sterna but cannot otherwise be distinguished from that of *T. tectus*.

*Pupa*.—Unknown.

*Material examined*.—Sixteen larvae (12 entire, 4 slide-mounted specimens, TAM, USNM), from pods of *Astragalus beckwithii* T. & G., collected 1 June 1972, 2.5 miles southeast of Provo, Utah County, Utah, determined by association with adults collected on the plants.

*Discussion*.—*Tychius semisquamosus* occurs in the Rocky Mountain region of the western United States and adjacent portions of Canada, and in southern California (Clark, 1971 and 1977). Its known hosts are all species of *Astragalus* in native American groups (Clark, 1977).

*Tychius soltaui* Casey

*Tychius soltaui* Casey, 1892:416.

*Tychius hirsutus* Clark, 1971:30 (replacement name for *T. hirtellus* LeConte, 1876:218; not Tourmier, 1873).

*Larva*.—The larva of *T. soltaui* is indistinguishable from that of *T. tectus*, except for possession of subcutaneous pigment on the ocellar areas. It is distinguished from the larva of *T. semisquamosus* only by the lack of conspicuous asperities on the thoracic and abdominal sterna.

*Pupa*.—The pupa of *T. soltaui* differs from that of *T. tectus* by having 1 instead of 2 femoral setae.

*Material examined*.—Thirty-one larvae (20 entire, 11 slide-mounted specimens, TAM, USNM), which emerged from pods of *Astragalus nuttallianus* A., D.C., collected 10 April 1973, 0.7 miles southeast of San Diego, Duval County, Texas, and from pods of *A. emoryanus* (Rydb.) Cory, collected 31 May 1973, 35 miles south of Alpine, Brewster County, Texas, determined by association with reared adults.

*Discussion*.—*Tychius soltaui* occurs in the western United States and adjacent portions of Canada (Clark, 1971) and in the state of Durango, Mexico (Clark, 1977). Its known hosts are species of *Astragalus* in native American groups (Clark, 1977). The relationship of *T. soltaui* to the other American species of *Tychius* associated with *Astragalus* was considered in the discussion of *T. tectus*.

#### *Tychius prolixus* Casey

*Tychius prolixus* Casey, 1892:419.

*Larva*.—The larva of *T. prolixus* is indistinguishable from that of *T. tectus*. It is distinguished from larvae of *T. semisquamosus* and *T. soltaui* by the absence of subcutaneous pigment from the ocellar areas.

*Pupa*.—The pupa of *T. prolixus* differs from that of *T. tectus* only in possession of 2 instead of 1 pair of meso- and metathoracic posteronotal setae. Some of the specimens examined have 1, but most have 2 femoral setae, as in *T. tectus*.

*Material examined*.—Twenty-one larvae (11 entire, 10 slide-mounted specimens, TAM, USNM), which emerged from pods of *Astragalus utahensis* (Torr.) T. & G., collected 1 June 1972, at the mouth of Rock Canyon, northeast of Provo, Utah County, Utah, and from pods of *A. wootonii* Sheldon, collected 30 May 1973, 6.5 miles east of the junction of Highways 505 and 166, Jeff Davis County, Texas, and 15 pupae (TAM, USNM), reared from larvae from the *A. utahensis* lot, all determined by association with reared adults.

*Discussion*.—*Tychius prolixus* occurs in southern California, Nevada, Utah, Arizona and western Texas (Clark, 1971). Its known hosts are species of *Astragalus* which belong to native American groups (Clark, 1977). Significance of characters by which *T. prolixus* and other *Astragalus*-

associated species are distinguished from each other was considered in the discussion of *T. tectus*.

*Tychius quinquepunctatus* L.

Fig. 3

*Curculio 5-punctatus* L. 1758:383.

*Tychius 5-punctatus* Germar, 1817:340.

*Larva*.—Body: 4.8–6.5 mm long (8 larvae); shining, yellow. Head (Fig. 3): Uniformly dark brown; rounded posteriorly; width of head capsule 1.23–1.30 mm (2 larvae). Anterior ocellar areas with minute spot, or without subcutaneous pigment. Accessory appendage of antenna robust. Endocarina more than  $\frac{1}{2}$  as long as frons. Dorsal epicranial seta 1 long, located well posterior to frontal suture. Posterior epicranium with 3 pairs of minute setae. Median labral sensillum present. Malar area of maxilla with 5 ventral setae, 4 dorsal setae, and 1 ventral sensillum. Labial palpus with 1 sensillum; glossa with 2 pairs of minute setae; postmental seta 1 present. Thorax: Pronotum with 5 long setae, 2 shorter setae, and 1 minute seta in addition to 2 minute anterolateral setae. Spiracle bicameral. Postdorsum of mesothorax and of metathorax each with 3 setae, of which seta 1 is long, seta 2 shorter, seta 3 longer than 1. Pedal area of each thoracic segment with 3 long and 2 short setae. Sternal seta long, subequal in length to ventral-most pedal seta of same segment. Abdomen: postdorsum with 3 long setae of subequal length. Spiracular seta 1 long, seta 2 shorter. Epipleural seta 1 longer than seta 2. Pleural seta 1 longer than seta 2.

*Pupa* (from Scherf, 1964, Fig. 238).—Length: 5–5.3 mm. Head: 2 pairs of frontal setae. Pronotum: Anterior-most pair of anterolateral setae located beside anteromedian setae, 2nd pair displaced posteriorly, behind subapical constriction of pronotum; 2 pairs of posterolateral setae present. Mesonotum and Metanotum: each with only 1 pair of posteronotal setae. Abdomen: Terga 1–8 each with 1 pair of discotergal setae. Legs: Femora each with 2 setae.

*Material examined*.—Ten larvae (8 entire, 2 slide-mounted specimens, USNM), labeled "*Tychius quinquepunctatus*, 209, Erlangen Rosenhauer," were examined. Identity of these specimens cannot be verified as there are no associated adults.

*Discussion*.—This European species reportedly has hosts in the papilionoid genera *Lathyrus*, *Phaseolus*, *Pisum* and *Vicia* (Scherf, 1964). The larva is distinguished from larvae of other known species of *Tychius* by the following combination: Glossa with 2 pairs of minute setae; malar area of maxilla with a ventral sensillum; postdorsum of mesothorax and of meta-

thorax with 3 setae, seta 1 long, seta 2 short, seta 3 longer than 1. The pupa has 2 femoral setae, 1 pair each of mesonotal and metanotal setae, and terga each with 1 pair of discotergal setae.

Larvae and pupae of *T. quinquepunctatus* have more in common with larvae and pupae of *T. sordidus*, *T. lineellus*, and the *Astragaleae*-associated species (*T. semisquamosus*, *T. tectus*, *T. soltau* and *T. prolixus*) than with those of the clover seed weevils (*T. stephensi* and *T. picirostris*) and that of *T. flavus* (Table 1). The only other species of *Tychius* known to have a sensillum on the malar area of the larval maxilla is *T. lineellus*; *T. picirostris* is the only other known species with only 1 pair of mesonotal setae. Adult characters do not indicate that *T. quinquepunctatus* is closely related to either of these, however, and it is likely that both similarities are due to convergence.

? *Tychius flavicollis* Stephens

*Tychius flavicollis* Stephens, 1831:56.

*Larva*.—As described for *T. tectus*, except as follows. Body: White. Head: Width of head capsule 0.52 mm (1 larva); rounded posteriorly. Endocarina  $\frac{2}{3}$  length of frons. Dorsal epicranial seta 1 long, located posteriorly distant from frontal suture. Mandibular setae long. Thorax: pronotum with 5 long setae and 3 short setae, in addition to 2 minute anterolateral setae. Pedal area of prothorax with 3 long and 2 short setae; pedal areas of mesothorax and metathorax each with 3 long setae and 3 short setae. Abdomen: Postdorsum with 3 setae, setae 1 and 3 short, seta 2 long.

*Pupa*.—Unknown.

*Material examined*.—Two larvae (1 entire, 1 slide-mounted specimen), labelled Schonebeck, a.d. Elbe 21-8-1931, C. Urban, (USNM) were examined.

*Discussion*.—No adults are associated with the specimens described here, so their identity is questionable. The specimens were apparently transmitted to the USNM from Urban, their collector. Urban (1935) reported finding larvae of *T. flavicollis*, along with larvae of *T. meliloti*, in the fruit of *Melilotus alba* Lam. Perris (1877), however, cited by Hoffman (1954) and Scherf (1964), stated that larvae of *T. flavicollis* develop in seeds of *Lotus corniculatus* L. Lengerken (1941) stated that *T. meliloti* develops in galls on the leaves of *Melilotus macrorhiza* Pers., and Hoffmann (1954) adds *M. alba* and *M. officinalis* (L.) to the list of hosts of that species.

There is indirect evidence that the larva described above as *T. flavicollis*



is not that of a Trifolieae-associated species, and is therefore possibly correctly associated with the species Franz (1942) called *T. flavicollis*. Franz considered *T. flavicollis* to be related to *T. kulzeri* Penecke, *T. cinnamomeus* Kiesenwetter and *T. cretaceus* Kiesenwetter. *Tychius cretaceus* was listed as synonym of *T. cinnamomeus* by Hoffmann (1954) who listed *Dorycnium suffruticosus* Vill. as the host of the weevil. The genera *Dorycnium* and *Lotus* belong to the papilionoid tribe Loteae (Hutchinson, 1964). Since closely related species of *Tychius* usually have closely related hosts, it is likely that Franz's *T. flavicollis* is a species associated with the plant genus *Lotus*. The tribes Loteae and Trifolieae are considered to be closely related (Hutchinson, 1964). Adult characters, however, indicate that *T. flavicollis* is also closely allied to the Trifolieae-associated *Tychius* (specimens of *T. flavicollis* as well as specimens of Trifolieae-associated species determined by Franz himself have been examined). The larva described above, however, shows greater affinity to larvae of Astragaleae-associated *Tychius*, than to those of the Trifolieae-associated *T. picirostris*, *T. stephensi* and *T. flavus* (see discussions of these below). Clark (1977) noted that *T. flavicollis* resembles the American Astragaleae-associated *T. liljebladi* Blatchley.

*Tychius stephensi* Schönherr

Fig. 9

*Curculio picirostris* Fabricius, 1787:101.

*Curculio tomentosus* Herbst, 1795:278 (not Olivier, 1790:536).

*Tychius stephensi* Schönherr, 1836:412.

*Tychius stephensi* Schönherr. Stephens, 1839:229.

*Larva*.—As described for *T. tectus*, except as follows. Body: 2.74–3.59 mm long (8 larvae); opaque, white. Head: Width of head capsule 0.41–0.48 mm (5 larvae). Ocellar areas with subcutaneous pigment. Dorsal epicranial seta 1 long. Clypeal setae moderately long. Median labral sensillum present. Malar area of maxilla with 5 ventral setae and 3 dorsal setae. Labial palpus with 2 sensilla; glossa with 2 pairs of minute setae. Thorax (Fig. 9): Pronotum with 4 long setae, 2 slightly shorter setae and 2 minute setae, in addition to 2 minute anterolateral setae. Spiracle unicameral, air tube with 4 or 5 annuli. Postdorsum of mesothorax and of metathorax with 2 setae, seta 1 moderately long, seta 2 longer. Pedal area of each thoracic segment with 3 long setae. Abdomen (Fig. 9): Postdorsum with 2 setae, seta 1 long, seta 2 shorter. Pleuron with 1 long and 1 short seta.

*Pupa*.—Unknown.

*Material examined.*—Six slide-mounted and numerous whole specimens labelled “Minnesota, St. Paul, 25 June, 1948, A. Peterson, ex heads red clover” (OSU), determined by association with adults preserved with larvae, were examined. These are the specimens upon which Peterson (1951) based his description of the larva of *T. stephensi*.

*Discussion.*—Introduced from Europe into North America, *T. stephensi* develops in the fruit of red clover, *Trifolium pratense* L. It is known as the red clover seed weevil in America. Although it has been called *T. stephensi* (sometimes *T. stephensi*) in America, in Europe it is known as *T. tomentosus* Herbst. As Clark (1971) pointed out, neither name is strictly correct since the types of both are conspecific with the type of *Curculio picrostris* Fabricius, 1787. Schönherr (1825) misidentified Fabricius’ *C. picrostris* and applied the name *picrostris* to the species commonly known in Europe and America as *Miccotrogus picrostris*. Since *Miccotrogus* is now in synonymy with *Tychius*, the appropriate combination is *Tychius picrostris* (Fabricius), following Clark (1976). A proposal to the International Commission on Zoological Nomenclature suggesting a solution is in preparation.

The larva of *T. stephensi* is distinguished from the other known *Tychius* larvae as follows: Thoracic spiracle unicameral, postdorsum of mesothorax and of metathorax, as well as of each abdominal segment, with 2 setae. The larva of *T. picrostris* is distinguished from that of *T. stephensi* by the bicameral thoracic spiracle, absence of the median labral sensillum, the short dorsal epicranial seta 1, possession of a single pleural seta on the abdominal segments, only 2 long pleural setae on the mesothorax and metathorax, and generally shorter thoracic and abdominal setae throughout.

Larvae of at least 2 other species of *Tychius* with hosts in the papilionoid tribe Trifolieae, *T. flavus* and *T. meliloti*, also have unicameral thoracic spiracles. The larvae of these do not differ from the larva of *T. stephensi* in any known characters. If the close resemblance of the larvae of the Astragaleae-associated species described above to each other is any indication of the way closely allied species of *Tychius* may be expected to differ, the larvae of *T. stephensi*, *T. flavus* and *T. meliloti* may in fact be difficult, if not impossible, to distinguish. Larvae of all 3 of these also have in common with *T. picrostris* most observed characters, including several (2 sensilla on labial palpus, 4 long pronotal setae, 2 thoracic and abdominal postdorsal setae and 3 dorsal setae on malar area of maxilla) not shared by the other known *Tychius* larvae. These shared characters support the contention that the Trifolieae-associated *Tychius* form a monophyletic group. Some of the members of this group, including *T. picrostris*, were formerly assigned to *Miccotrogus* (see Clark, 1976).

*Tychius picirostris* (Fabricius)

Fig. 11

*Miccotrogus picirostris* (Fabricius). Schönherr, 1825:583, and subsequent authors, based on misidentification of *Curculio picirostris* (Fabricius, 1787).

*Tychius picirostris* (Fabricius). Clark, 1976.

*Larva*.—As described for *T. tectus*, except as follows. Body: 1.78–2.81 mm long (8 larvae); opaque, white. Head: Width of head capsule 0.43–0.44 mm (2 larvae). Ocellar areas with subcutaneous pigment. Dorsal epicranial seta 1 minute. Clypeal setae minute. Median labral sensillum absent. Malar area of maxilla with 5 ventral setae and 3 dorsal setae. Labial palpus with 2 sensilla; glossa with 2 pairs of setae, without sensilla. Thorax (Fig. 11): Pronotum with 4 long setae, 2 slightly shorter setae, and 2 minute setae, in addition to 2 minute anterolateral setae. Spiracle bicameral, air tubes of unequal length. Postdorsum of mesothorax and of metathorax with 2 setae, seta 1 short, seta 2 longer. Pedal areas of mesothorax and of metathorax with 2 long setae and 1 shorter seta. Abdomen (Fig. 11): Postdorsum with 2 setae, seta 1 long, seta 2 short. Pleuron with 1 moderately long seta.

*Pupa*.—Length: 1.14–1.28 mm. Head: 2 pairs of frontal setae, 1 pair small, each seta borne on small tubercle located slightly anterior and mesal to larger pair of tubercles which bear much stouter, longer setae. Pronotum: Anterior-most pair of anterolateral setae located beside anteromedian setae, 2nd pair displaced posteriorly to apical  $\frac{1}{4}$  of pronotum; 1 pair of posterolateral setae. Posteromedian setae more widely separated than discal setae. Abdomen: Terga 1–8 each with 1 pair of discotergal setae. Legs: Devoid of setae.

*Material examined*.—Ten larvae (8 entire, 2 slide-mounted specimens TAM, USNM) and 3 pupae (TAM, USNM) collected in eastern Washington or western Idaho, by Yunus and Johansen, determined (by Johansen) by association with adults reared from white clover seeds, were examined.

*Discussion*.—This European species, like *T. stephensi*, has been introduced into North America where it is a pest of clover seed. It is called the clover seed weevil. Its biology was studied by Yunus and Johansen (1967). Hosts in North America are white clover, *Trifolium repens* L., and alsike clover, *T. hybridum* L. Problems of the nomenclature of this species and the red clover seed weevil are reviewed above in the discussion of *T. stephensi*.

The larva of *T. picirostris* is distinguished from the other known *Tychius* larvae as follows: Thoracic spiracle bicameral; median labral sensillum and glossal sensilla absent; and pedal area of mesothorax and of metathorax

each bearing 2 long setae and 1 shorter seta. The pupa is distinguished by possession of 1 pair of posterolateral pronotal setae, 2 pairs of posteronotal setae on the meso- and metathorax, 2 pairs of discotergal setae on the abdomen, and absence of femoral setae.

Comparisons of the larva of *T. picirostris* and of the related *T. stephensi*, *T. flavus* and *T. meliloti* and hypotheses concerning relationships of these to each other and to other *Tychius* are set forth above in the discussion of *T. stephensi*.

### *Tychius flavus* Becker

*Tychius flavus* Becker, 1864:488.

*Larva*.—Servadei (1947) provided fairly good illustrations and description of the larva of *T. flavus*, from which the following diagnosis is taken: Length 2.5–3.0 mm; head brown, endocarina  $\frac{1}{2}$  as long as frons; dorsal epicranial seta 1 long; median labral sensillum present; malar area of maxilla with 3 ventral setae, and 9 (?) dorsal setae; postmental seta 1 present; pronotum with 6 long setae (this probably indicates 4 long and 2 slightly shorter setae); all spiracles unicameral; postdorsum of mesothorax and that of metathorax with 2 setae; pedal area of each thoracic segment with 3 long setae; postdorsum of typical abdominal segments each with 2 setae.

Scherf's (1964) description and illustrations of the larva of *T. flavus* are apparently adapted from those of Servadei (1947). These are not as complete as those of Servadei, however, and some inconsistencies are noted. For example, Scherf illustrated an extra frontal seta, and omitted the median labral sensillum. Servadei's description and illustrations are more in line with our observations on members of the genus *Tychius*. Unfortunately, neither Scherf's nor Servadei's descriptions are complete enough to permit some important comparison (e.g. relative setal lengths, number of sensilla on the labial palpalae and glossa).

*Pupa*.—Scherf (1964, Fig. 244) also reproduced Servadei's (1947) illustration of the pupa of *T. flavus* (which unfortunately included only a ventral view) and gave a brief description. From these the following diagnosis is derived: Length 2.0–2.5 mm; rostrum devoid of setae; 1 pair of frontal setae present, interocular and supraocular setae absent; apparently 3 pairs of anterolateral pronotal setae present; legs each with 2 femoral setae.

The identity of the specimens examined by Scherf and Servadei has not been verified.

*Discussion*.—This European species develops in pods of *Medicago sativa* L. (Scherf, 1964). It is a serious pest of seed production of this important

forage crop in Europe. Its biology was studied by Tanasijevic (1955) and by Ionescu et al. (1965).

The only character mentioned by Servadei (1947) by which the larva of *T. flavus* differs from the larvae of the other *Tychius* with unicameral thoracic spiracles (*T. picirostris* and *T. meliloti*) is the number of ventral setae on the malar area of the maxillary palpus, which Servadei (1947:159, Fig. XVII) depicted as no fewer than 9; we observed not more than 5 ventral malar setae in the species examined. Servadei's (1947) description of the pupa is too brief to be of value in making comparisons.

### *Tychius meliloti* Stephens

*Tychius meliloti* Stephens, 1831:55.

*Larva*.—Scherf (1964) provided a brief description, without illustration, of the larva of *T. meliloti*. This agrees with our generic description but, aside from showing that the thoracic spiracles are unicameral, it is not of further taxonomic value.

*Pupa*.—Scherf's (1964) description of the pupa of *T. meliloti* omits important diagnostic characters but does indicate that it has the following: Length 2.5–2.8 mm; rostrum with 1 pair of basirostral setae and 1 pair of interocular setae; head with 1 pair of frontal setae; pronotum with 6 pairs of setae; abdomen apparently with 2 pairs of discotergal setae. No mention is made of femoral setae.

*Discussion*.—Urban (1935) reported that this European species develops in fruit of *Melilotus alba* and *M. officinalis*. Scherf (1964) also listed *M. altissimus* as a host.

The unicameral larval thoracic spiracle and the host association indicate that *T. meliloti* is closely allied to 2 of the other Trifolieae-associated species, *T. stephensi* and *T. flavus*, as considered in the discussion of *T. stephensi*. The pupa is apparently like that of *T. picirostris* in possessing only a single pair of posterolateral pronotal setae.

### *Tychius crassirostris* Kirsch

*Tychius crassirostris* Kirsch, 1871:48.

*Larva*.—Mik (1885) and Scherf (1964) presented brief descriptions and illustrations of the larva of *T. crassirostris*. These agree with our generic description, but do not contain information diagnostic at the species level.

*Pupa*.—Mik (1885) illustrated a ventral view of the pupa of *T. crassirostris*. Scherf (1964) reproduced the figure and from it wrote a brief description. According to Scherf the pupa is 2.8–3.4 mm long. The figure indicates that the setae on the head are as illustrated for *T. sordidus*

(Fig. 12), except that the lowermost basirostral seta is actually "distirostral" in position. One pair of frontal setae are present. The pronotum apparently has 3 pairs of anterolateral setae, the abdomen only a single pair of discotergal setae. The legs each bear 1 femoral seta.

*Discussion.*—Mik (1885) and Urban (1935) give accounts of the life history and habits of this European species whose larvae develop in galls on the leaves of *Melilotus alba*. Scherf (1964) lists other *Melilotus* as well as *Medicago* hosts.

The larva of *T. crassirostris* is poorly known. The pupa is evidently like those of *T. flavus* and *T. meliloti* in possessing 3 pairs of anterolateral pronotal setae, and like that of *T. picirostris* in having only a single pair of posterolateral pronotal setae.

### Taxonomic Relationships

Although only a small proportion of the total number of species of *Tychius* (13 out of more than 300) are known from the immature stages, some general statements concerning taxonomic relationships based on characters of these stages can be made. Characters of the larvae and pupae of some species appear to support some groupings indicated by adults and host plant relationships. A comprehensive evaluation of character states of the adults for recognition of monophyletic groups in *Tychius* has yet to be carried out, however; and we have not attempted to determine relative apomorphy-pleiomorphy in the characters of the relatively small sample of immatures studied.

Distributions of character states of larvae and pupae diagnostic at species level in *Tychius* are presented in Tables 1 and 2, respectively. Diagnostic characters for larvae include differences in relative lengths of setae on the head capsule, thorax and abdomen, presence or absence of setae and sensilla on the mouthparts, and numbers of chambers in the thoracic spiracles. Presence or absence of pigment on the ocellar areas, and presence or absence of asperities on the sternal areas of the thoracic and abdominal segments also appear to distinguish some species, but others exhibit variation in these features. Pupae of species of *Tychius* differ from each other in numbers of pairs of anterolateral and posterolateral pronotal setae, mesonotal and metanotal setae, discotergal abdominal setae, and in presence or absence and numbers of femoral setae. Some of these pupal characters are variable within the small samples examined.

*Trifolieae-associated species.*—The most distinctive grouping indicated by larval characters includes *T. stephensi*, *T. picirostris*, *T. flavus* and *T. meliloti*, all of which have hosts in the papilionoid tribe Trifolieae (*Trifolium*, *Melilotus* and *Medicago*). The existence of a monophyletic Trifolieae-associated group within the genus *Tychius* was postulated by

Clark (1976). The known larvae of members of this group are distinguished as follows: Malar area of maxillary palpus with 3 dorsal setae; labial palpus with 2 sensilla; glossa of labium with 2 pairs of setae; pronotum with 4 long setae; mesothorax and metathorax each with 2 postdorsal setae. Some of these character states are shared by other *Tychius* larvae, but none have them in the same combination. Only 1 Trifolieae-associated species, *T. picirostris*, is known in sufficient detail in the pupal stage to permit meaningful comparisons. The pupa of this species, and apparently that of *T. meliloti*, are distinguished from other *Tychius* pupae by possession of only 1 pair of posterolateral pronotal setae.

The larva of *T. picirostris* differs from known larvae of other Trifolieae-associated *Tychius* in the short dorsal epicranial seta 1, absence of the medial labral sensillum and short abdominal pleural seta 1. It is also unique among Trifolieae-associated species in possession of bicameral thoracic spiracles, a feature which it shares with all known non-Trifolieae-associated *Tychius* larvae.

*Tychius flavicollis*.—Adult characters and host relationships indicate that the other *Tychius* whose immature stages are known represent at least 5 different infrageneric groups (see Clark, 1976 and 1977). These groups are more homogeneous in the immature stages than the Trifolieae-associated group, however (Tables 1 and 2). The adult of *T. flavicollis* resembles adults of Trifolieae-associated species, but it also resembles some adults of a group of species associated with members of the papilionoid tribe Astragaleae, most notably the American *T. liljebladi* (see Clark, 1977). The larva of *T. flavicollis*, however, does not differ from larvae of Astragaleae-associated species in any of the characters studied (the pupa is unknown). The host of *T. flavicollis*, *Lotus corniculatus*, belongs to Loteae, a papilionoid tribe which Hutchinson (1964) considered to be more closely related to Trifolieae than to Astragaleae.

*Tychius quinquepunctatus*.—On the basis of adult characters, *T. quinquepunctatus* appears to be closely allied to species assigned to the genera *Apeltarius* Desbrochers and *Xenotychius* Reitter. The larva of *T. quinquepunctatus* differs from larvae of Astragaleae-associated *Tychius* only in possession of 2 rather than 1 pair of setae on the glossa of the labium. It differs from the larvae of *T. sordidus* and *T. lineellus* only in characters which it shares with Astragaleae-associated species. It has 2 pairs of glossal setae on the labium, like Trifolieae-associated *Tychius*. The pupa of *T. quinquepunctatus* also shows affinity to Trifolieae-associated species in possession of a single pair of posterolateral pronotal setae. Characters of the adults of *T. quinquepunctatus* and of Trifolieae-associated species, however, do not indicate that the 2 groups are closely related. Known hosts of *T. quinquepunctatus* belong to the genera *Pisum* and *Vicia*, mem-

bers of the tribe Viciae, a tribe which Hutchinson (1964) considers to be closely allied to the tribe Trifolieae.

*Astragaleae-associated species*.—Monophyly of this group whose members occur in North America and Eurasia was postulated by Clark (1977) on the basis of adult characters and host relationships. Members of the group with known immature stages, *T. tectus*, *T. semisquamosus*, *T. soltau* and *T. prolixus*, have nearly identical larvae. They differ from each other in presence or absence of pigment on the ocellar areas and presence or absence of asperities on the sternal areas of the thorax and abdomen. These differences are minor and of doubtful taxonomic value. The pupa of *T. soltau* has 1 instead of 2 femoral setae, but it is otherwise indistinguishable from known pupae of other Astragaleae-associated species, which in turn are indistinguishable from each other.

*Tychius lineellus* and *Tychius sordidus*.—Adult characters indicate that these North American species represent 2 distinct but related species groups (Clark, 1977). Larvae of the 2 species differ in several respects. The larva of *T. lineellus* differs from all known *Tychius* larvae, except those of Trifolieae-associated species, by possessing 2 sensilla on the labial palpus. This similarity is probably the result of convergence; adult *T. lineellus* in no way resemble adults of Trifolieae-associated species, and the hosts of *T. lineellus* (species of *Lupinus*, tribe Lupineae) are not closely related to the Trifolieae. The head of the larva of *T. lineellus* (Fig. 2) also has several distinct features not listed in Table 1, namely the head capsule is deeply emarginate posteriorly, the accessory appendage of the antenna is long and slender and dorsal epicranial setae 1 and 3 are relatively short (cf. *T. sordidus* Fig. 1). In adult characters *T. lineellus* appears to be more closely allied to the European *T. venustus* (Fabricius) than to any American *Tychius* (see Clark, 1977). The larva of *T. sordidus* differs from that of *T. lineellus* and larvae of Astragaleae-associated species in the relatively long setae on the alar area of the thoracic segments and on the epipleural folds of the abdominal segments. The pupa of *T. sordidus* is unique among known *Tychius* pupae in possessing 2 pairs of discotergal setae on abdominal terga 1–8.

Status of *Miccotrogus* Schönherr.—One of the species whose immatures are described herein, *T. picirostris*, along with several other European *Tychius*, were previously assigned to a separate genus, *Miccotrogus* Schönherr, because they have 6 instead of 7 antennal funicular articles. The North American *T. prolixus*, although never formally assigned to *Miccotrogus*, also has 6 funicular articles. After examining adult morphological characters and host relationships of several Old World and American species, Clark (1976) concluded that *Miccotrogus* was polyphyletic, and he placed that name in synonymy with *Tychius*. The immatures of *T. picirostris* and of



*T. prolixus* have nothing in common which would justify their separation from other *Tychius* examined. We conclude, therefore, that Clark's (1976) hypothesis of polyphyly is not refuted by characters of the immatures described herein. It should be noted, however, that although immatures of *T. prolixus* differ only in minor respects from those of other Astragaleae-associated *Tychius*, the larva and pupa of *T. picirostris* are distinguished from other Trifolieae-associated *Tychius* by several features (see discussion of Trifolieae-associated species).

### Conclusions

It is often claimed that characters of the immature stages of weevils and other insects should or do contribute to knowledge of phylogeny (see Emden, 1957; Ahmad and Burke, 1972; Pfaffenberger and Johnson, 1976). It is true that the immature stages provide a set of attributes which theoretically have as much potential for revealing monophyletic groups as do adult structures. Some authors have noted the lack of congruence between classifications based on characters of immatures and those based on adults (see Rohlf, 1963; Pfaffenberger and Johnson, 1976). It seems to us that any 2 systems (e.g. morphological, karyotype, behavioral, biochemical, etc.) may differ to the extent that purely phenetic classifications based on them will be incongruent. However, we feel that what is needed in systematic studies is that all systems be analysed, the evidence drawn from each synthesized into a unified system, preferably a phylogenetic one. This is the essence of Hennig's (1966) holomorphological method. The attributes of different developmental stages should be considered of equal value in phylogenetic analysis to the extent that similarities are not the results of parallelism or convergence.

We have observed larvae and pupae of several members of the subfamily Tychiinae (those treated herein, those of *Sibinia sulcatula* (Rogers et al., 1975), and of other species of *Sibinia* which will be described elsewhere, and those of *Neotylopterus pallidus* (LeConte) (Clark, 1978b), as well as immatures of members of several other subfamilies (including published accounts by Emden, 1938; 1952; Ahmad and Burke, 1972; and others listed by Burke and Anderson, 1976). For the most part, character states of these have yet to be rigorously analysed with the express intent of recognition of synapomorphies. Instead, analyses have been of the sort presented in the previous section; i.e., recognition of groups on the basis of subjectively weighted similarity. From the present study of tychiines and from our general familiarity with curculionid immatures, it is expected that the search for synapomorphy, at least at and below the generic level, will be fraught with difficulty. This is because attributes observed up to now, and upon which most studies, including the present one, are based (differences

in numbers, positions and relative lengths of setae, variation in numbers of chambers in the spiracles) are, for the most part, of the sort that one worker (Schlee, 1969) referred to as "simple features poor in structure and having only a few details." It is generally agreed that with such characters it may be difficult to distinguish similarity due to common ancestry from similarity resulting from parallel or convergent development.

Nevertheless, we do not advocate abandonment of the search for synapomorphies in the larvae and pupae of tychiines and other weevils. It is quite possible that patterns and combinations of the kinds of characters examined in the present study will prove to be of greater value in determining relationships at higher levels. Other systems such as internal anatomy (see May, 1967 and 1977) are also likely to contribute useful information. Furthermore, the host and other biological information usually obtained while collecting immatures has already been shown to be of value as evidence of phylogenetic relationships in the Curculionidae.

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#### Footnote

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